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Adaptation to Dynamic Environments Displays Local Generalization for Voluntary Reaching Movements

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***Abstract* — The shape of the directional generalization function for adaptation to a viscous force-field environment has been controversial. Some studies have suggested wide, essentially global generalization and others have suggested narrow, local generalization. Here, we show definitively that motor adaptation displays narrow generalization with a minimal global component and a peak at the trained movement direction for both single-trial and asymptotic adaptation. Furthermore, we find that reaching movements in opposite directions do not interfere with one another during force-field learning.**

I. Introduction

Learned motor skills exhibit generalization – the ability to transfer learning from the trained condition to new situations. Generalization across movement directions describes the extent to which the learning of an adaptation transfers from one movement direction to another.

Although generalization functions (GFs) for force-field (FF) adaptation have been studied in the past [1-6], previous studies have yielded conflicting results. In one group of studies, GFs were not measured directly after adaptation but were instead inferred using highly parameterized state-space models of trial-by-trial adaptation [2,4-5]. The large number of parameters fitted in these models of trial-by-trial adaptation suggests that overfitting may be an issue. In line with this idea, very different shapes have been reported for the GF, ranging from entirely local [2-3] to essentially global [2] to intermediate [4]. A second group of studies [1,6-7], have examined movement trajectories after adaptation and consistently found local generalization. The variance between these two sets of results and the finding that multiple adaptive processes underlie motor adaptation have led to speculation that trial-by-trial and extended learning display different patterns of generalization.

Here, we directly measured adaptive changes in motor output during individual probe trials when (1) opposing FFs were learned in different movement directions, and after (2) extended and (3) single-trial learning of a single FF in order to better understand the GFs for learning physical dynamics.

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II. Methods

A. Participants and General Task Description

All experimental participants were naïve to the experimental purpose, provided informed consent and were compensated for their participation. Subjects performed quick (peak speed = 0.32±0.03 m/s) point-to-point reaching arm movements while holding the handle of a 2-link robotic manipulandum. In certain movements, the subjects' trajectories were perturbed laterally by the viscous curl FF described in Equation 1:

$$\vec{F}(\vec{v}) = \boldsymbol{B}\vec{v} = b\begin{bmatrix} 0 & 1 \\ -1 & 0 \end{bmatrix}\begin{bmatrix} v_x \\ v_y \end{bmatrix} \quad (1)$$

On a subset of trials, we measured adaptive changes in motor output by using an error clamp [8-11] to essentially eliminate lateral errors, so that force profiles comprising feedforward adaptation could be measured independently of feedback responses. In short, we compared the lateral force profile displayed on each trial with the force profile that would have fully compensated the imposed FF in order to assess the level of adaptation. We quantified this comparison with a normalized adaptation coefficient obtained from regressing the measured force profile onto the ideal force profile. This is essentially equivalent to the normalized projection of each measured force profile onto the ideal force pattern. This results in adaptation level estimates that are similar to, but somewhat more consistent than those obtained from simply normalizing the mid-movement force.

B. Experiment 1: Adaptation Interference Across 180°

Forty-one neurologically intact individuals (mean age = 21.0±2.7 years; 20 male) were recruited for Experiment 1. After a baseline period, subjects were presented with viscous FFs for 150 movements in two movement directions (90° and 270°). Twenty-one subjects experienced the same FF in both the 90° and 270° directions (either clockwise (CW; b=15 N/(m/s)) or counterclockwise (CCW; b=-15 N/(m/s)) in both directions), and the other 20 experienced opposite FFs (CW in one direction and CCW in the other). We compared the learning curves of these two groups (Fig. 1).

C. Experiments 2 & 3: Extended Training Generalization

Forty-five neurologically intact individuals (mean age = 28.6±10.7 years; 20 male) were recruited. After a baseline period, participants were presented with a viscous FF in the 90° direction for 125 trials (Experiment 2). Subjects were randomly assigned to one of three different FFs: CW, CCW, or null (b=15, -15, or 0 N/(m/s), respectively). All of the 270° movements during the training phase were error clamp trials. After completing the training period, the generalization of learning was assessed in 34 directions distributed around the unit circle (Experiment 3).

D. Experiment 4: Single-trial Training Generalization

Twenty-nine neurologically intact individuals (mean age = 21.2±4.3 years; 12 male) were recruited. Subjects first experienced a baseline period during which no perturbations were present. After this period, subjects experienced sparse random CW (b=15 N/(m/s)) and CCW (b=-15 N/(m/s)) FF perturbations for a single trial in the 90° movement direction. We measured the generalization elicited by 168 of these trials in 12 movement directions (0°, 30° … 330°), with 8 repeats per FF and per direction.

III. Results

A. Learning of Motor Skills in Opposite Directions Occurs Independently

If FF learning does not generalize to movements in the opposite direction, there should be no interference when simultaneously learning different FFs in opposite movement directions. We compared subjects who learned the same versus opposite FFs in opposite movement directions when making alternating movements between these two directions, and found essentially identical learning curves ($p > 0.5$) as shown below in Fig. 1.

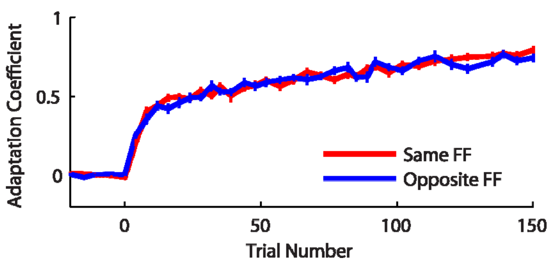

Fig. 1. Adaptation to the same and opposite force-fields progresses at the same rate. Simultaneous learning of opposite force-fields in movements 180° apart progresses at the same rate as learning of the same force-field in both movement directions.

B. Learning of a Motor Skill in a Particular Direction Does not Lead to Learning in the Opposite Direction

In a second experiment we measured the level of adaptation 180˚ away from a single training direction to directly assess the amount of generalization 180˚ away. Comparison of the adaptation coefficients between trained and untrained movement directions (Fig. 2) reveals that adaptation occurs in the trained direction, but not the untrained direction. In the trained movement direction, we find clear learning curves for both active FFs, and no clear learning for the Null FF (Fig. 2A).

Along the untrained movement direction, we see a small downward trend in the learning curves for all three conditions (Fig. 2B), but no clear difference between groups. When we combine the learning curves for the CW and CCW FFs to look at the adaptive changes specific to the trained dynamics (Fig. 2C), we see a clear learning curve in the trained direction ($p < 0.001$), but we find that the adaptation in the untrained direction is not different from zero even late in training ($p > 0.24$). This indicates a lack of generalization 180˚ away from the training direction, which is consistent with the results of Experiment 1.

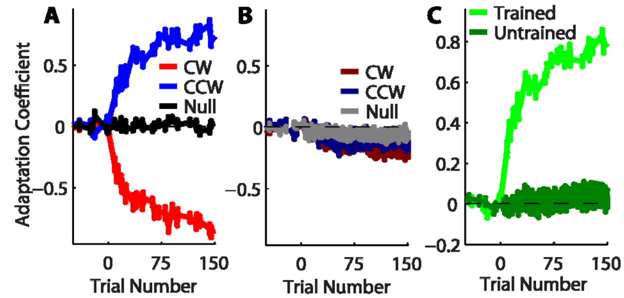

Fig. 2. Adaptation curves in the trained direction and 180° away shows that adaptation does not generalize across 180°. (A) Adaptation curves for a trained movement in a CW, CCW, and null field. (B) Adaptation curves in the untrained return direction, 180° away from the trained direction. (C) Combined adaptation curves for the trained and untrained directions for adaptation to CW and CCW FFs.

C. Direct Measures of Generalization Show that both Initial and Extended Learning are Local

In order to examine the amount of generalization at locations other than 180˚ away from the training direction, we conducted two additional experiments where we measured generalization after single-trial adaptation and extended adaptation. In both the single-trial (Fig 3A) and extended training (Fig 3B) experiments, we found unimodal Gaussian-shaped GFs, with peaks at the training direction and very similar widths (σ=37.8˚ for the single-trial GF versus σ=38.7˚ for the extended training GF).

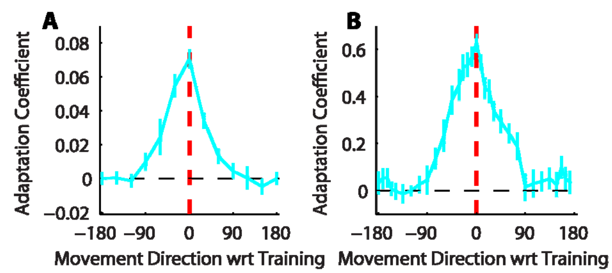

Fig. 3. Generalization during both initial and extended learning is local to the trained direction. (A) The generalization function of initial learning has a similar width (σ=37.8°) to (B) the generalization function of extended learning (σ=38.7°).

IV. Discussion

In this study we investigated how motor adaptation generalizes. We show that GFs for FF adaptation are local (σ=35-40˚), with essentially no generalization of learning 180° away from the trained movement direction. This provides insight into the neural representation of motor adaptation [8, 12-14]. These findings are at odds with previous work in which global generalization functions were often obtained from fitting highly parameterized state space models of trial-by-trial learning to complex data sets in which adaptation and unlearning were randomly interleaved across movement directions [2]. We show that the GFs for single-trial adaptation and extended learning have similar widths (σ=37.8˚ and 38.7˚, respectively), and are well characterized by unimodal Gaussian functions. In summary, these results indicate that generalization is local, and that there is little difference in the width of generalization for the fast and slow adaptive processes in motor adaptation [11].

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